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VOLUME XLIX NUMBER 2

BOTANICAL GAZETTE

FEBRUARY 1910

THE EFFECT OF CERTAIN CHEMICAL AGENTS UPON THE TRANSPIRATION AND GROWTH OF WHEAT SEEDLINGS

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(WITH NINE FIGURES)

The physiological factors involved in transpiration present numerous opportunities for critical study. A vast number of researches upon these factors have been made and our knowledge has been increased thereby; nevertheless the results of some important pieces of work are contradicted by others and more data seem to be necessary to elucidate certain questions.

The present paper is intended to set forth some data upon the effect of certain chemical compounds (mostly salts) upon the transpiration of wheat plants in relation to the effect of the same compounds upon the growth of the plants. In other words, the paper is in part a study of the effect of these compounds upon the units of water transpired for unit of plant substance produced.

The general literature bearing upon the effect of chemicals upon transpiration has been so well brought together and summarized by BURGERSTEIN (2) that a general review of literature need not be given at this place. A few studies which have especial bearing upon the present work, however, will be mentioned.

LAWES (6) made a careful investigation of the amount of water required by several plants grown to maturity, where possible, in sealed pots of soil. He used in one series soil to which no application of fertilizing compounds was added; in the second series a mineral fertilizer consisting of potassium sulfate, magnesium sulfate, sodium chlorid, and mono-calcium phosphate was added to the soil; in the third series the mineral fertilizer used in the second series was supplemented with ammonium chlorid. In each series wheat, barley, beans, peas, and clover were grown. The third series having the ammonium chlorid failed to make satisfactory growth, but the other two yielded data of interest.

The application of the mineral fertilizer to soil in which wheat was grown diminished the amount of water required for the production of a unit of dry matter, and the mineral plus ammoniacal fertilizer diminished the amount still farther. The same relations held in the case of peas and clover. On the contrary, the amount of water transpired per unit of dry matter in beans was somewhat increased where the mineral fertilizer was present, and the same was true to a rather small extent in the case of barley, but only when the mineral fertilizer plus ammonium chlorid was present.

The experiments of SACHS (**12**), which have become classical, consisted in adding pure chemicals to sand, earth, or solution in which a plant was growing, and carefully observing the effect on the transpiration for a few days. In some experiments the supply of water in the soil was replenished after a few days, in others it was not. It was observed that the addition of KNO_3, $(NH_4)_2SO_4$, or gypsum to the soil decreased the amount of transpiration compared with that of a similar plant in control soil. Similarly, the addition of NaCl or $(NH_4)_2SO_4$ to distilled water decreased transpiration. A small amount of HNO_3 added to distilled water caused a great increase in transpiration, but a small amount of KOH caused retardation.

The investigations of BURGERSTEIN (**1**) confirmed the statements of SACHS and others in finding that acids accelerate transpiration and alkalies retard it. Solutions of calcium nitrate, potassium nitrate, potassium phosphate, potassium carbonate, ammonium nitrate, ammonium sulfate, magnesium sulfate, and sodium chlorid were tried, and all found to increase transpiration up to a certain point.

The observations of MAERCKER (**10**) upon the effects of potash fertilizers showed that the application of substances like kainit and carnallit has an effect upon the water requirement of white mustard. In his experiments the plants were grown in an artificial soil in large zinc pots. The soil, which consisted of sand containing 2.5 per cent. of peat, received the raw potash salts at the rate of 1000 and

2000^{kg} per hectare. In one set of experiments the soil received 60 per cent. of its capacity, and in another set 27 per cent. The effect of these treatments was found to be as follows:

Soil containing 60 per cent. of its water capacity. Treatment	Relative amounts of water required to produce one unit of dry weight	Soil containing 27 per cent. of its water capacity. Treatment	Relative amounts of water required to produce one unit of dry weight
No potash salts............	100.0	No potash salts............	100.0
1000^{kg} kainit per hectare...	90.5	1000^{kg} kainit per hectare...	77.1
2000^{kg} kainit per hectare...	88.4	2000^{kg} carnallit per hectare.	68.9
2000^{kg} carnallit per hectare.	91.9		

The economizing influence of the potash salts naturally showed itself more strongly upon the soil which contained the smaller proportion of water.

The pots in MAERCKER'S experiments were not sealed to prevent loss of water from the surface of the soil; his figures therefore represent the total amount of water evaporated from the soil directly and through the activity of the plants, but they show very distinctly a tendency toward economy in water absorption where the potassium salts were applied.

HARTWELL, WHEELER, and PEMBER (5) have also reported that the application of potassium chlorid to wheat seedlings in soil causes an increase in green weight relatively larger than the increase in transpiration. In nutrient solutions it was found that sodium usually had a similar effect in retarding transpiration in comparison with growth.

GARDNER (3) has reported results which also show that the general effects of fertilizers applied to soils in pots was to increase in various ratios the amount of green weight in proportion to the water transpired.

SORAUER (15) and HARTER (4) have reported the results of experiments in which a large amount of soluble salt was added to soil or solution and the effect upon transpiration noted. The large amounts of salts which they employed produced halophytic conditions with corresponding changes in the anatomy of the plants, therefore their results will not be compared with those which follow in this paper, because in them the amounts of salt added were not sufficient to alter materially the concentration of the soil solution.

The data to be presented in this paper were drawn from upward of 6000 tests employing soils, soil extracts, and salt solutions. The data showing the effects of treatments upon soils were obtained from experiments which employed 189 soils from various parts of the United States. These data were obtained in the course of fertility tests made by the Bureau of Soils of the U. S. Department of Agriculture, and were kindly furnished by Mr. F. D. GARDNER, who was in charge of the work; the other data are drawn from experiments made by the author while a member of the staff of that bureau's laboratory.[1]

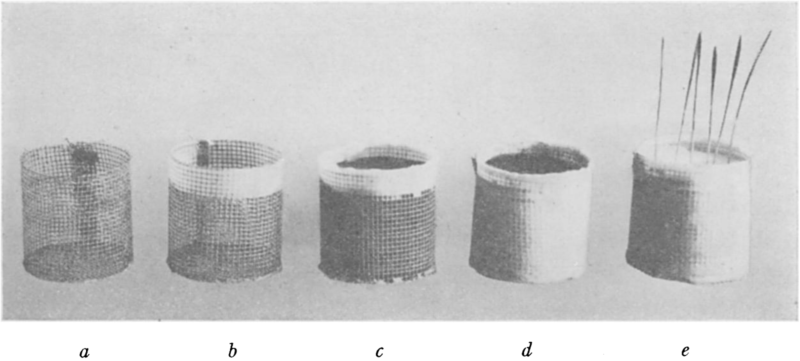

FIG. 1.—Method of making paraffined wire pots: *a*, wire frame; *b*, same with rim of paraffin; *c*, same filled with soil; *d*, completed pot, having wall formed by repeated dipping in melted paraffin; *e*, pot containing plants four days old and showing the cover of paraffined paper sealed to rim of the pot.

All tests conducted with soils were made in the standard paraffin wire pot employed extensively for experimental work in plant physiology and agronomy. As an instrument of research it commends itself especially because of its easy construction and its ability to yield accurate experimental results.[2]

The method of making these pots is illustrated by *fig. 1*. The framework of wire netting is 10^{cm} in diameter and of the same height (*a*). After coating the rim of the framework by dipping several times in melted paraffin (*b*), the pot is filled slightly above the edge of the paraffined rim with soil which has received enough water to place it in optimum condition (*c*). The pot is then dipped in melted paraffin with intermediate cooling until a firm wall is formed (*d*). At the first dipping the paraffin penetrates a short distance into the soil and thus cements the outer surface of the mass of soil to the wall of the pot. A straight, shallow furrow is then made across the surface of the soil and the seeds planted in it. In the present work, where wheat was used, it was previously soaked in tap water until undoubted signs of germination were shown and seven seeds were planted in each pot. If seven plants appeared above the surface of the soil, one was subsequently removed, leaving six to grow in each pot. It is advisable to cover the surface of the soil in the pot with a layer of clean sand to prevent a crust from forming on the soil, as well as to aid in uniformly distributing the water which is added. The pots are carefully weighed on the day of planting, when the soil is in the optimum moisture condition, and their weight recorded. A few days after the plants appear above the surface of the soil, the pot is sealed by covering the top with a circular piece of paraffined paper provided with a narrow slit in a position which allows the row of plants to pass. The paper is sealed to the inner surface of the wall of the pot with paraffin. Such a pot is shown at *e* in *fig. 1*. The pot is weighed immediately before and after sealing, and the increase of weight due to the addition of paper and paraffin is added to the initial weight recorded as the "optimum" for each pot. The paraffined paper prevents the loss of all but a very slight amount of moisture by evaporation from the soil. Since it is transpiration relative to control cultures and not absolute transpiration which was determined, the small amount of water lost through the slit may be neglected. Thereafter distilled water is added in sufficient quantity at intervals of three or four days to keep the weight of the pots near that of the original. When water was required by the pots, it was introduced through the slit in the paraffined paper cover by means of a pipette.

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[1] For making most of the computations upon which this paper is based, I am indebted to my wife, HANNAH D. REED.

[2] This method finds commendatory mention in GANONG'S *Plant physiology*, 2d ed., 1908, p. 173.

One of the conspicuous points of superiority which the paraffined wire pot possesses over the ordinary pot with a non-adhesive wall is shown in *fig. 2*. In experiments of this character, where the effect of soil treatment is to be estimated by the result upon plant growth, it is essential that the roots of the test plants be living within the soil instead of being external to it. *Fig. 2* shows at the left the soil mass from a paraffined wire pot, and at the right that from a pot with a non-adhesive wall. Wheat plants had grown in each pot for three weeks at the time the photograph was made. In the paraffined pot the plant roots were entirely restricted to the soil mass, while in the other pot the absorbing region of a majority of the roots was external to the soil and hence not indicating response to the treatment given to that soil.

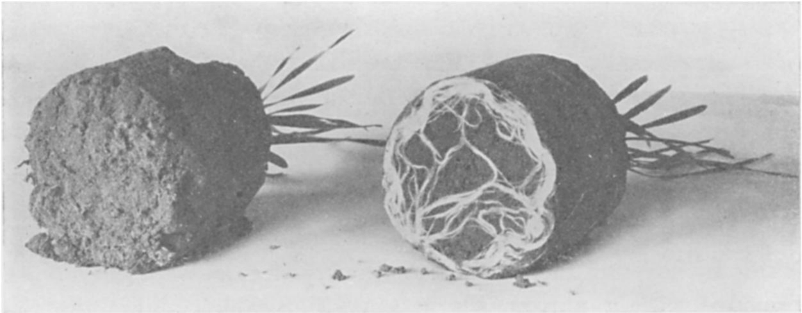

FIG. 2.—Root distribution in paraffined wire pot and in ordinary pot; on the left is shown the contents of a paraffined wire pot, and on the right those of an ordinary pot.

During the course of an experiment the pots were kept in situations where the conditions of heat and light were as nearly uniform as possible.

The exact duration of the different experiments naturally varied somewhat on account of external factors, but was usually 18 to 21 days. During very hot summer weather the period was often somewhat shortened; the best conditions for growth in Washington, D. C., being found in the months of May and September. In order to eliminate errors which might unavoidably arise, as well as inherent differences in individual plants, five pots, each containing six seedlings, were used for each test; therefore, in recording the effect of any treatment, the total transpiration and green weight of the 30 plants distributed in five pots were taken. The total transpiration was determined by summing up the total losses of water from the pots during the experiment; the green weight was found by cutting the plants at the surface of the soil in the pot and weighing them immediately, before any material loss of water occurred. If the dry weight was to be recorded, the plants from each set of pots were placed in unsealed paper envelopes and slowly dried at room temperature.

Many experiments described in this paper were carried out in water cultures, in which the aqueous extract of a soil, or a salt solution was used as the culture fluid. The water cultures were prepared and conducted according to the methods described by LIVINGSTON (**8**) and SCHREINER and REED (**14**), in which 10 wheat seedlings are installed in each culture jar. The culture jars employed in this work were saltmouth green flint glass bottles of 240^{cc} capacity. Flat corks which fitted the mouths of these bottles were notched by cutting ten vertical wedges from their lateral surface. Each wedge was about 4^{mm} broad and 5 or 6^{mm} deep, and extended from top to bottom of the stopper. The cork wedges, after being cut out, were truncated at their inner angles by the removal of enough cork to allow them to be replaced in position after a seedling had been placed in the inner apex of the space from which each wedge had been cut. The stem of the seedling was placed in its groove, with the seeds just below the lower surface of the cork, and the wedges were pressed into position. Each wedge should exert sufficient pressure on the seedling to hold it in place when the stopper is inserted in the bottle. After all were in position, a rubber band was placed around the stopper to hold the wedges in place, and the stopper was then pressed firmly into the neck of the bottle which contained the culture fluid. The cultures prepared by this method afford practically no opportunity for the direct evaporation of water from the bottles. Practically all the water lost occurs as transpiration from the plants grown in the cultures. To keep conditions equable, the solution in the bottles should be renewed or the bottles replenished with distilled water every four or five days.

Since the water loss is only through the plants, the cultures may be weighed at each change, and the sum of the losses recorded may be taken as the total transpiration of the 10 plants for the period of the experiment. This total water loss being proportional to the leaf area when wheat is used, it is consequently a practical method for comparing growth of several cultures when grown simultaneously under the same conditions.

It seems not improper to point out that, under these conditions of experiment, the water content of the medium in which the plants were grown was very nearly constant during the period of the experiment, a condition which has been lacking in many experiments upon transpiration. SACHS, for example, supplied water to the soil at the beginning of an experiment, but usually added no additional water during the course of the experiment.

Most of the studies recorded in this paper are based upon the amount of water transpired per gram of green substance produced under different conditions of experimentation, a factor which in the present study is designated "correlative transpiration."

In most of the experiments involving the use of soil, four different chemical compounds were used, viz., nitrogen as sodium nitrate, potassium as potassium sulfate, phosphorus as mono-calcium phosphate, and calcium as calcium carbonate. The first three salts were applied to the soils, where used, at the rate of 100 parts to a million of soil, but calcium carbonate was added at the rate of 1000 parts per million of soil. To facilitate accuracy and rapidity, the first three salts were applied in the form of solutions, but the calcium carbonate was added in a dry, finely ground condition.

A general survey of the data presented in the following pages shows that, in the majority of cases, the plant growth was increased by the addition of various compounds commonly used as fertilizers in agricultural practice. The paper by GARDNER (3) contains extensive data upon this point, all of which were obtained by the use of the paraffined wire pot. GARDNER'S data are consonant in showing an increase in plant growth. Some of the soils employed were what might be termed unproductive soils; their unproductiveness, however, was in some cases due rather to the presence in them of deleterious compounds than to actual poverty in nutrient substances. Others of the soils he employed were productive. Naturally the increases due to the addition of fertilizer compounds were greater in the former class of soils.

The studies under consideration in this paper relate to the transpiration correlated with growth as affected by the addition of definite chemical agents to the soil or solution in which the plants were grown.

Experimental results

STUDIES ON THE TRANSPIRATION OF PLANTS GROWN IN SOILS

The first data presented deal with the average effect of the four different salts upon the transpiration of plants grown in 189 soils from different localities.

The untreated pots used as controls exhibited an average transpiration of 103.3^g water for each gram of green weight produced. In the pots where the salts were added the amounts of water transpired per gram of green weight were: $NaNO_3$, 93.36^g; K_2SO_4, 97.95^g; $CaH_4(PO_4)_2$, 104.07^g; $CaCO_3$, 101.09^g. Using the transpiration of the controls as a basis and representing it as 100, the different treatments would have the following values: $NaNO_3$, 90.40 per cent.; K_2SO_4, 94.80 per cent.; $CaH_4(PO_4)_2$, 100.8 per cent.; $CaCO_3$, 97.9 per cent.

These figures show that at least two of the four salts employed were responsible for a proportionally diminished transpiration. In the case of the other two, the differences from the control were not so great, in fact in the case of mono-calcium phosphate the units of water used were almost precisely the same as in the controls. It may be said in passing that in individual cases the economy of water used was much greater than would appear from the average result. For example, one sample of Crawford clay, to which $NaNO_3$ was added, showed only 69 per cent. as many units of water required for a unit of growth as in the untreated soil, at the same time growth was increased 31 per cent. Also, in a sample of Portsmouth swamp soil, to which K_2SO_4 was added, the units of water required for a unit of growth were only 71.2 per cent. of what was required in the controls, while growth was increased 112 per cent.[3]

Since the introduction of extraordinarily low figures brought down the average figures, I next made an investigation of the amounts of water transpired in experiments where the salts had a slight influence upon growth and also in experiments where influence was large. I selected for this purpose two classes of results, in one of which the effect of the added salt upon the green weight of the plants was so small as to be doubtful, and in the other there was a distinct acceleration. In the first class of results the response as measured by green weight varied between 95 and 105, and is regarded as doubtful response, since a variation of only 5 per cent. above or below the controls may be regarded as within the limit of error. In the other class of results the response was 120 or greater, and therefore includes cases in which there was undoubted acceleration.

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[3] In this connection it may be said that the opposite relation was sometimes observed, namely, an increased consumption of water when growth was diminished by the addition of a salt. In a sample of Memphis silt loam, to which K_2SO_4 was added, the resulting growth was but 91 per cent. of that in untreated soil, while the water required per unit of growth was 17 per cent. more than in the controls.

A summary of the results of these tests is presented in table I. Each computation is the average of 25 tests, with the exception of no. 1, which is the average of 20 tests.

TABLE I

EFFECT OF VARIOUS SALTS UPON TRANSPIRATION OF WHEAT PLANTS IN CASES WHERE THE CORRELATED EFFECT UPON THE GROWTH WAS VERY SMALL AND IN CASES WHERE IT WAS DISTINCTLY INCREASED. SALTS ADDED TO SOIL IN WHICH PLANTS GREW

No.	Salts added	Green weight of plants grown in soils receiving the salt. Controls = 100 in each case	Units of water transpired per unit of green weight. Controls = 100 in each case
1	$NaNO_3$	100.25	95.3
2	"	130.00	84.0
3	K_2SO_4	101.00	94.0
4	"	128.00	86.0
5	$CaH_4(PO_4)_2$	100.16	100.4
6	"	128.00	95.5
7	$CaCO_3$	100.5	99.9
8	"	142.0	99.0

These results may be regarded as giving added light to those previously presented. They show that in the case of $NaNO_3$ and K_2SO_4 there was greater economy of water used the greater the effect upon growth as indicated by the green weight. In the case of $CaH_4(PO_4)_2$ and $CaCO_3$, it has already been shown that their inhibiting effect upon transpiration is much inferior to that of $NaNO_3$

and K_2SO_4. In the case of $CaH_4(PO_4)_2$, as shown in table I, there is, however, a slight decrease in the units of water required for a unit of green weight where the growth response was greater. In the case of $CaCO_3$ the difference is too slight to warrant any statement one way or the other.

The relations between green weight and transpiration are further illustrated by the graphic representation given in *figs. 3, 4*, and *5*. To construct the curves there shown I selected from each set of experimental data an ascending series of green weights. These figures ranged, as shown, from a value slightly less than that of the controls to a value indicating a growth approximately twice as great as that of the controls. The control for each one is represented by 100, therefore the position of the points above or below 100 on the chart represents the effect of the salt which was added to the soil in that particular series of experiments.

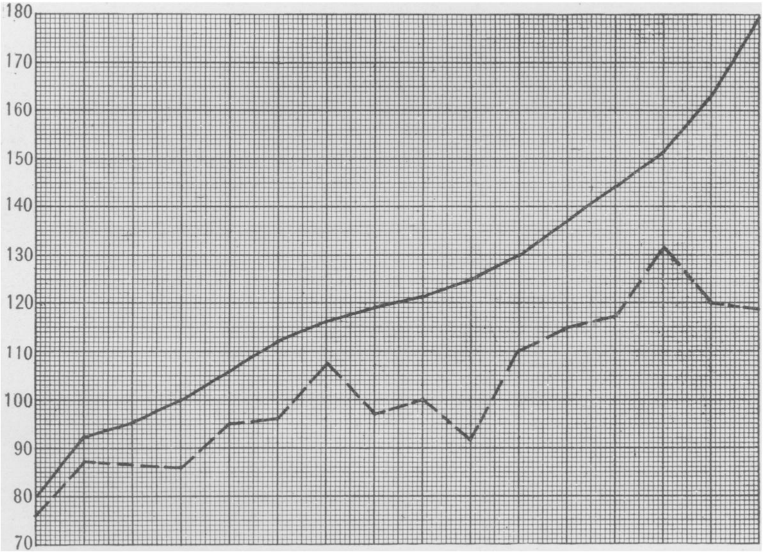

FIG. 3.—Correlative growth and transpiration in soils to which K_2SO_4 was added; in all charts the continuous line represents green weight, and the broken line transpiration.

Arranging the figures representing the green weights in an ascending order, I let the respective transpiration figures fall as they might.

The transpiration was estimated in each case by comparison with the transpiration of the control plants, the transpiration controls being also represented as 100. By joining these points, a curve was obtained representing the rise and fall of the transpiration in comparison with the somewhat steady rise of the green weight in these selected cases. In all charts green weight is represented by the continuous line and transpiration by the broken line.

In selecting these figures, care was taken to omit all in which the results might appear to be large on account of very small growth in the control. Had such been included the results would have been even more striking than they stand.

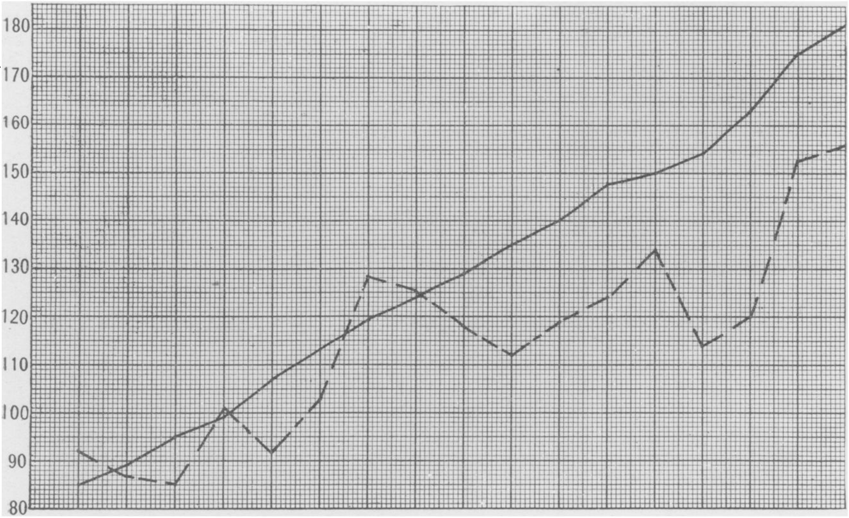

FIG. 4.—Correlative growth and transpiration in soils to which $NaNO_3$ was added.

An inspection of *fig. 3* shows that potassium sulfate in particular acts as an economizing factor (agent) in transpiration. In this case the curve representing the transpiration of the plants lies entirely beneath the green weight curve. The transpiration curve rises as the green weight curve rises but the rise is not exactly parallel. This fact harmonizes with the relation brought out in a preceding paragraph dealing with the relative quantities of water required where the corresponding increase in green weight was small and where it was large. In the lower part of the figure, where the green weight is near 100, the two curves lie closer together and more nearly parallel than in the upper part of the figure. From these relations it appears that the transpiration per unit of green weight is smallest when the acceleration of growth caused by the application of K_2SO_4 was greatest.

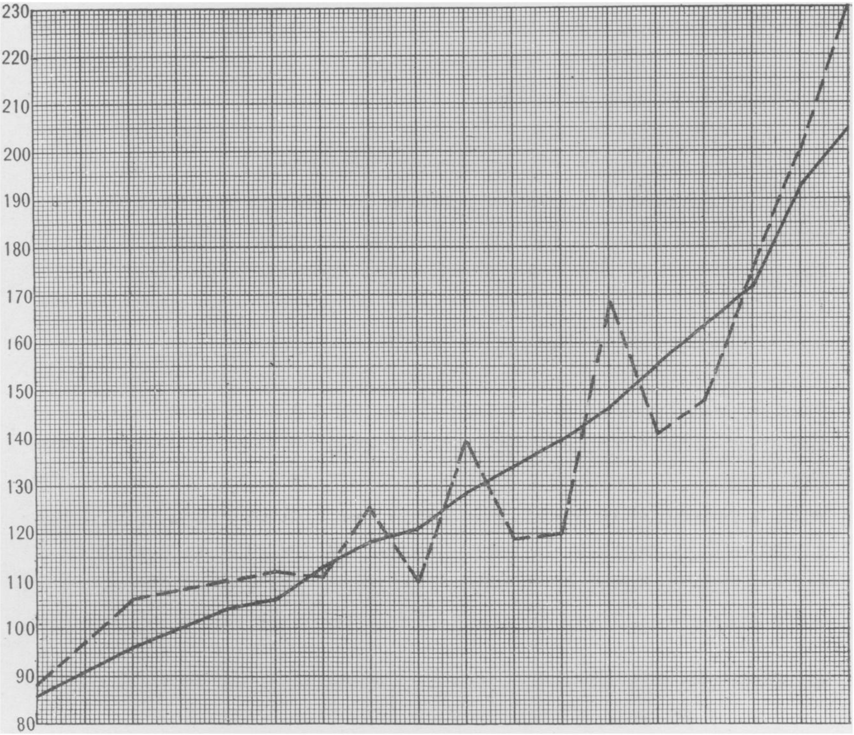

FIG. 5.—Correlative growth and transpiration in soils to which $CaCO_3$ was added.

Fig. 4 shows curves constructed in a similar way to show the action of sodium nitrate upon green weight and transpiration. As before, the numerical values representing the green weight of the various experimental plants are arranged in an ascending series. The curve representing the transpiration of the plants is somewhat more irregular than in the case of the K_2SO_4 experiments, yet its mean position lies somewhat below the green weight curve. This is interpreted to mean that the transpiration of plants grown in pots to which $NaNO_3$ was added was relatively less than the correlated green weight; in other words, that the influence of the $NaNO_3$ was to reduce the amount of water required per unit of green weight.

In the lower part of the figure the mean of the transpiration curve lies closer and more nearly parallel to the green weight curve than in the upper part. This relation is in harmony with the facts previously presented in showing that the economizing action of the $NaNO_3$ was greater where the greatest acceleration in growth was produced (compare table I).

Fig. 5 likewise represents similar relations between green weight and the transpiration in experiments where calcium carbonate was added to the soils. A brief inspection suffices to show that the mean curve of transpiration lies very close to the green weight curve. In the lower part of the figure the transpiration curve is slightly above that for green weight; however, the mean of the former curve approximates closely that of the green weight.

Contrary to the relations exhibited by the two preceding pairs of graphs, the transpiration curve does not perceptibly diverge from the green weight curve in the upper part of its course; thus showing that increased growth due to the action of this salt was not correlated with a reduction of water transpired per unit of green weight produced. This relation is corroborated by the results presented in table I, where the units of water transpired per unit of green weight were scarcely different in cases of low response and high response.

STUDIES ON THE GROWTH AND TRANSPIRATION OF PLANTS GROWN IN SOIL EXTRACTS AND SOLUTION CULTURES

A comparative set of experiments was carried out by the use of aqueous soil extracts as a medium for plant growth. The extracts were made by stirring one part soil with five parts non-toxic distilled water. The mixture was stirred five minutes, allowed to stand thirty minutes, and then filtered through a Pasteur-Chamberland filter. This method gives a good, clear soil extract and is easily employed. Salts were added to the soil extracts and their effect upon transpiration observed as in the case of the pot experiments in which soil was used. As in the case of the former series of experiments, there was, on the aggregate, increased growth, resulting from the addition of salts commonly used as fertilizers. A few cases in each series gave growth somewhat less than the controls and others were practically equal to the controls, but a goodly number in each series gave material responses in the positive direction. On account of a smaller number of experiments, not so many comparisons are possible, however, as in the case of the former series.

One feature associated with the growth of wheat plants in soil extracts or nutrient solutions is deserving of especial mention. When the compounds added to a medium caused (as many of them did) a material increase in root growth, there was usually a corresponding increase in transpiration, regardless of whether the growth of the green parts of the plants was greatly increased or not. It is held that the increase in size of the absorptive system is connected in some way with an accelerating action upon the escape of water from the subaerial portions of the plant.

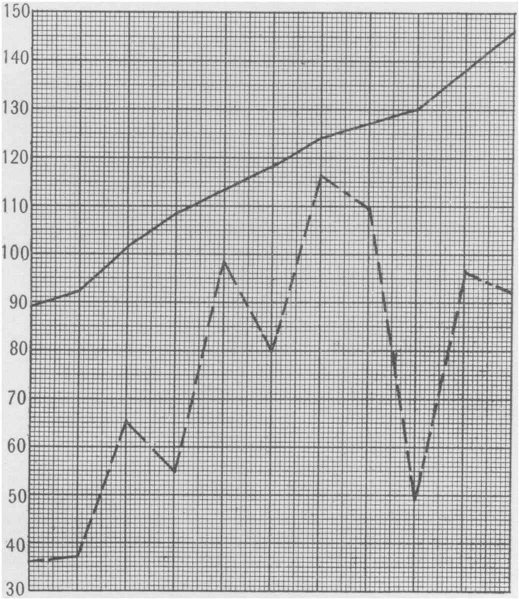

FIG. 6.—Correlative growth and transpiration in soil extracts to which K_2SO_4 was added.

The first computations are concerned with the units of water required to produce a unit of green weight, and the influence of various compounds thereupon.

The plants grown in soil extract to which sodium nitrate was added showed a transpiration per unit green growth 96.7 per cent. of transpiration in the controls. Similarly, the transpiration in soil extract plus potassium sulfate was 85.3 per cent.; in extracts plus sodium phosphate, 110 per cent.; in extracts plus calcium carbonate (saturated solution), 163 per cent. of the controls.

In the former series of experiments there was no comparison between the sodium and the potassium salts of the same acid. A few comparisons were made in this series of experiments employing K_2SO_4 and Na_2SO_4, the results of which are of some interest, since one of the salts functions as a plant nutrient and the other probably does not. In the comparison at present under consideration it was found that plants grown in soil extracts receiving sodium sulfate exhibited a transpiration per unit of green weight equal to 93.9 per cent. that of the controls, whereas an equivalent amount of potassium sulfate added to extracts of the same soils and in which plants were simultaneously grown gave 85.3 per cent.

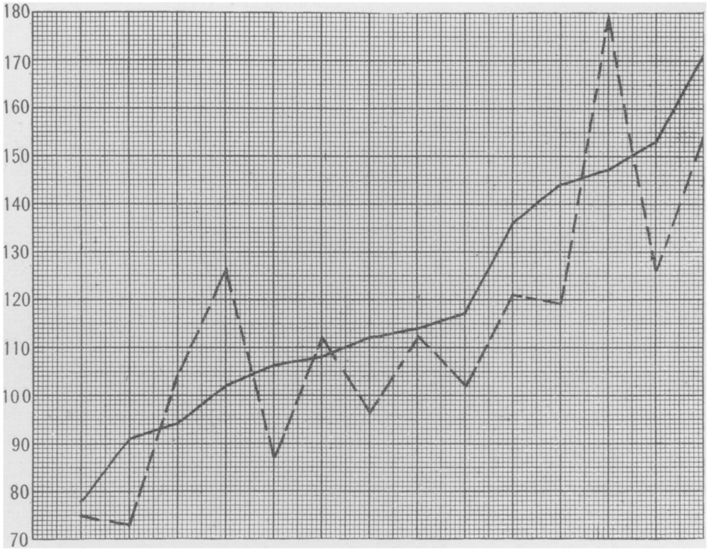

FIG. 7.—Correlative growth and transpiration in soil extracts to which $NaNO_3$ was added.

A comparison of the effects of two different salts of potassium was afforded by the results from the use of potassium chlorid and potassium sulfate in extracts of the same soil. Sixteen experiments were selected in which these two salts had been added to extracts of the same soil, and plants grown simultaneously.

The average transpiration for unit of green weight was 56.77^g in the controls, 34.81^g for KCl, and 34.05^g for K_2SO_4. Expressed in percentage of the controls, the addition of KCl caused a use of water amounting to 61.4 per cent. of the controls, and K_2SO_4 caused a use of water amounting to 60 per cent. of that used by the controls in untreated soil extract.

It appears, therefore, that potassium is more efficient than sodium in diminishing the transpiration per unit of green growth produced. Different salts of potassium did not exhibit wide variation in their inhibiting action upon transpiration. Sodium, however, is able, to some extent, to retard the transpiration per unit growth, and part of the retarding action of sodium nitrate is therefore attributable to the action of the sodium ion.

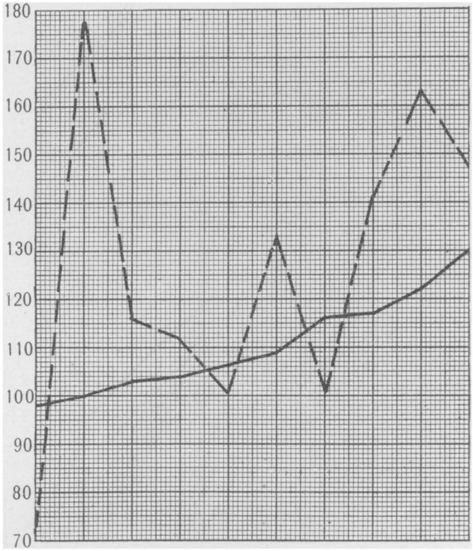

FIG. 8.—Correlative growth and transpiration in soil extracts to which Na_2HPO_4 was added.

The effect of adding these salts to soil extracts is shown by curves in *figs. 6, 7, 8,* and *9,* where the method of constructing the curves was similar to that used for *figs. 3, 4,* and *5.* In *fig. 6,* which shows the effect of K_2SO_4, it is evident that the correlative transpiration is much lower than the growth, since every point in this transpiration curve is below the green weight curve. The middle portion of the transpiration curve lies nearer the green weight curve than either of the extremities, but the general trend of this curve shows that constant retarding action upon transpiration in all cases whether the green weight of the plant was increased much or little.

The effect of $NaNO_3$, as shown in *fig. 7,* is not so marked in retarding transpiration. Here the mean of the transpiration curve lies very close to the green weight curve, and is generally parallel to it. The upper part of the transpiration curve, which lies somewhat below the green weight curve, may probably be regarded as showing a retardation of transpiration in those examples.

Fig. 8, showing the relationship between green weight and transpiration in cultures to which Na_2HPO_4 was added, may be regarded as a general indication of the effect of the PO_4 ion. The transpiration here appears to be generally higher than the correlative green weight and is accordingly consonant with former results.

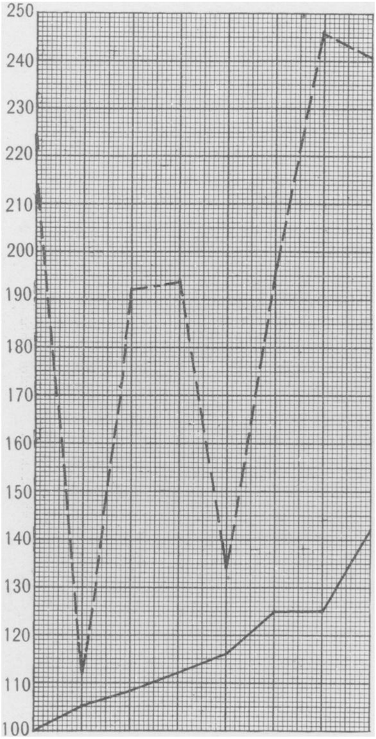

FIG. 9.—Correlative growth and transpiration in soil extracts to which $CaCO_3$ was added.

The effects of $CaCO_3$, as shown by the curves in *fig. 9*, is very accelerating upon transpiration. Although the transpiration curve is subject to somewhat extreme fluctuation, all its points lie above the green weight curve and the mean of the transpiration curve lies far above.

It may be said that, in the main, the salts had the same effect when added to soil extracts as when added to the soil in which plants were grown, although, in the case of $CaCO_3$ the results were somewhat more emphasized in the soil extracts.

The next studies taken up were devoted to the effect of acids and alkalies upon transpiration. This question has previously been studied by numerous investigators, notably SENEBIER, SACHS, and BURGERSTEIN, all of whom apparently agree in showing that the addition of a small amount of an acid increases the transpiration, while the addition of a small amount of alkali decreases transpiration.

In my experiments the acids or alkalies employed were added in smaller amounts than used by SACHS or BURGERSTEIN; and the experiments were extended for 12 to 15 days instead of 1 to 4 days, as in BURGERSTEIN'S experiments. The cultures were set up in duplicate with ten wheat plants to each culture.

In the two experiments first presented tests were made with organic and inorganic acids. The effect of these acids upon transpiration, green weight, and the correlation between the two is shown in tables II and III.

TABLE II

UNITS OF WATER TRANSPIRED PER UNIT OF GREEN WEIGHT IN WHEAT CULTURES CONTAINING VARIOUS AMOUNTS OF OXALIC AND ACETIC ACIDS

No.	Solution	Transpiration grams	Green weight grams	Units H_2O per unit green weight
1	Control in H_2O	64.5	1.47	43.8
2	$C_2H_2O_4$ $\frac{n}{2500}$	105.0	1.82	57.7
3	" $\frac{n}{5000}$	106.0	1.93	54.9
4	" $\frac{n}{10000}$	60.0	1.56	38.4
5	" $\frac{n}{20000}$	106.5	2.03	52.4
6	" $\frac{n}{40000}$	72.0	1.91	44.7
7	$CH_3 \cdot COOH$ $\frac{n}{2500}$	65.5	1.61	40.7
8	" $\frac{n}{5000}$	137.5	2.48	55.5
9	" $\frac{n}{10000}$	69.5	1.67	41.6
10	" $\frac{n}{20000}$	78.5	1.56	50.3
11	" $\frac{n}{40000}$	87.0	1.76	49.4

Several relations are indicated by the results presented in these tables. The figures indicate that the transpiration of the plants was slightly increased by the addition of small amounts of inorganic acids, and in most cases was perceptibly increased by the addition of the organic acids. The figures expressing the green weight show that the addition of acids generally increased the green weight, possibly excepting H_2SO_4 and the stronger solutions of HCl. This relation is perhaps due to the fact that these solutions proved injurious to growth as indicated by transpiration and green weight. When one examines the figures showing the units of water transpired per unit of green weight, he finds that the presence of inorganic acids in the concentrations there used did not cause an increase in the amount transpired per unit green growth, but caused instead a greater or less retardation in transpiration. In the experiments where organic acids were added the proportional transpiration, in most of the cases, was somewhat larger than that of control plants. Here then the results may be said to agree with those of the authors previously mentioned. But the results given in table III show quite general disagreement.

TABLE III

UNITS OF WATER TRANSPIRED PER UNIT OF GREEN WEIGHT IN WHEAT CULTURES CONTAINING VARIOUS AMOUNTS OF INORGANIC ACID

No.	Solution	Transpiration grams	Green weight grams	Units H_2O per unit green weight
1	Control in H_2O	53.0	1.46	36.3
2	HCl $\frac{n}{2500}$	26.0	.90	28.8
3	" $\frac{n}{5000}$	27.5	1.08	25.4
4	" $\frac{n}{10000}$	32.5	1.50	21.7
5	" $\frac{n}{20000}$	52.0	1.75	29.1
6	" $\frac{n}{40000}$	57.2	1.73	33.0
7	HNO_3 $\frac{n}{2500}$	35.5	1.40	25.3
8	" $\frac{n}{5000}$	46.5	1.61	25.1
9	" $\frac{n}{10000}$	61.5	1.84	33.4
10	" $\frac{n}{20000}$	59.5	1.75	34.0
11	" $\frac{n}{40000}$	47.5	1.67	28.4
12	H_2SO_4 $\frac{n}{2500}$	15.5	1.24	12.5
13	" $\frac{n}{5000}$	32.0	1.19	26.9
14	" $\frac{n}{10000}$	49.5	1.60	30.9
15	" $\frac{n}{20000}$	45.0	1.46	30.8
16	" $\frac{n}{40000}$	30.0	1.38	21.7

In attempting an explanation for these differences, attention may be directed first to the fact that the plants in my experiments were grown for longer periods of time in the acid solutions than those of the previous investigators, and the possibility exists that accelerated transpiration of these plants was temporary and would eventually have given place to a retardation. The plants upon which my observations were made had developed almost from germination in the solutions to be tested, since they were transferred to the solutions when the longest roots were 2–3^{cm} long.

The greatest reason for the apparent difference in results is believed to be due to the fact that the previous writers have taken no account of the correlated growth in measuring transpiration. Transpiration is probably a function of growth, and as such cannot be separated from it. It seems more correct, therefore, to estimate the effect of a treatment in terms of the transpiration per unit of green weight, or, since in my experiments the green weight was at the beginning of the experiment almost *nil*, to estimate the effect of the treatment in terms of the transpiration *per unit increase* in green weight.

THE ACTION OF ALKALIES

This problem was also studied by the earlier investigators in manner similar to that employed for studying the action of acids, which, as previously stated, is open to certain objections. The results of my experiments, which record the amount of transpiration per unit of green growth, disagree with those of the writers quoted. My experiments on this point were conducted upon wheat plants growing in water cultures, prepared by the methods previously described. The hydroxids of potassium and of sodium were present in these cultures in concentration of $n/100$; this involved the addition of 39 parts per million of K in the form of KOH, and 23 parts of Na as NaOH, amounts approximating those employed in the other experiments.

Table IV presents the average result of two experiments in which KOH and NaOH were added to extract of Hagerstown loam, a sample which was known to "respond" to potash fertilizers being used.

Unfortunately, the number of my observations is small, and it would be unsafe, therefore, to make any extended discussion of the results, although they are believed to be entirely consonant with the true state of affairs. So far as they go, they disagree with those of previous workers in showing that both the absolute and the relative amount of transpiration was increased by the addition of KOH and NaOH in small amounts. In these small amounts the effect upon growth appears to be distinctly beneficial. The transpiration per unit of green growth appears to have been increased slightly where the hydroxids were added.

TABLE IV

plants Effect of KOH and NaOH upon growth and transpiration of in extract of Hagerstown loam. Average of two experiments

No.	Solution	Transpiration	Green weight	Units water transpired per unit green weight
1	Untreated soil ext.	100	100	26.9
2	Soil ext. plus $\frac{n}{100}$ KOH	182	160	30.5
3	Soil ext. plus $\frac{n}{100}$ NaOH	157	138	29.2

The effects of pyrogallol and tannic acid were studied on plants grown in soil extracts. The addition to the extract of a soil, especially if it be an unproductive soil, of these substances which probably possess no nutrient value usually causes increased growth and greatly increased transpiration. The effects of small amounts of these substances is shown in table V, where the figures are the average of six experiments on soil taken from six different plots at one of the state agricultural experiment stations.

TABLE V

Effect of pyrogallol and tannic acid on soil extract. Average of six experiments

No.	Solution	Transpiration	Green weight	Units water transpired per unit of green weight
1	Control	100	100	100
2	Soil ext. plus 5 parts per million pyrogallol	160	109	139
3	Soil ext. plus 5 parts per million tannic acid	139	100	133

From these results it would appear that the pyrogallol and tannic were responsible for very marked increases in transpiration, without causing correspondingly marked increase in green weight, in fact the average effect of tannic acid shows no increase in green weight. Where the action of these compounds upon soil extracts has been studied, they have been found to accelerate principally two things, transpiration and root growth. In this respect their effect resembles that of manure extract, as has been pointed out by SCHREINER and REED (**13**). From a rather extended study of this phenomenon under various conditions, it seems only logical to conclude that pyrogallol in a soil extract acts to improve the conditions for growth by acting upon deleterious organic compounds present in those extracts. In non-toxic distilled water, similar effects are not observed. The improvement in growth conditions which follows the action of pyrogallol and other phenol derivatives is more quickly and markedly manifested by the roots than by the green parts of the plant (cf. the illustrations reproduced in the last-named publication). This point is well illustrated by an experiment whose results are presented in table VI. In this experiment pyrogallol was added at the rate of 2, 4, and 8 parts per million to extracts of two soils taken from the experiment grounds of an experiment station. Soil "A" was taken from a rich cabbage field; soil "B" was taken from an unproduc-

TABLE VI

EFFECT OF PYROGALLOL UPON ROOT GROWTH, TOP GROWTH, AND TRANSPIRATION IN TWO SOIL EXTRACTS

No.	Solution	Transpiration	Weight of entire plant	Weight of tops	Weight of roots*	Units water transpired per unit green weight
1	Extract of soil "A"	100	100	100	100	100
2	Same plus 2 p.p.m. pyrogallol	100	94	88	100	113
3	Same plus 4 p.p.m. pyrogallol	122	114	85	146	144
4	Same plus 8 p.p.m. pyrogallol	76	117	81	156	94
5	Extract of soil "B"	100	100	100	100	100
6	Same plus 2 p.p.m. pyrogallol	119	98	95	104	125
7	Same plus 4 p.p.m. pyrogallol	138	116	99	143	140
8	Same plus 8 p.p.m. pyrogallol	152	132	106	171	143

* The roots were taken from the solution, quickly dried between sheets of filter paper, and weighed. A small amount of capillary water was present, but the error is minimized by the fact that the figures given are comparative, not absolute.

tive timothy meadow. In estimating the results the weight of the roots and tops was separately taken.

These results show (with the exception of no. 4) a good correlation between transpiration and root growth. The order of responses is the same in the respective columns. In the case of no. 2, where no increase or decrease was observed in transpiration, a like relation is observed in the root growth. There was a slight increase, however, in the transpiration per unit of green growth, due perhaps to the fact that the green weight of these plants was below normal.

The general import of the experiments presented in tables V and VI seems to be that the addition of pyrogallol or tannic acid causes a marked acceleration in transpiration, and that this acceleration is correlated more with the growth of roots than of the green parts of the plant. As a consequence of this response, the amount of water transpired per unit of green weight appears larger than the response to any other agent used.

In many respects the growth of wheat plants in a soil extract previously treated with finely divided solids resembles that in extracts to which pyrogallol has been added. Undoubtedly the action of the two is similar in alleviating some unfavorable condition which previously existed, but was removed by the treatment in question. The pyrogallol must enter into chemical combination with some deleterious compounds in the soil extract or cause some process of oxidation, while the finely divided solids such as carbon black or ferric hydrate absorb and remove from solution the same deleterious substances. It is not proposed to dwell upon the general aspect of this problem in this place, since it has been treated in other papers and by various authors. The point to be demonstrated here is the effect of this treatment upon the transpiration per unit of green weight.

A large increase in transpiration is usually caused by the treatment with absorbing agents. In most cases, the substance employed as an absorbing agent was added to the soil extract, stirred or shaken frequently during a half-hour, and then filtered out before the extract was used as a culture medium for plants; but the same or slightly greater increases were produced by leaving the absorbing agent in the solution during the time the plants were growing.

Ordinary distilled water, which contains small amounts of poisonous metals from the distilling apparatus, together with small amounts of volatile organic substances which pass over in an ordinary still, may show similar amelioration by treatment with absorbing agents. A representative instance is shown in table VII; other cases have been given by LIVINGSTON (**9**).

TABLE VII

EFFECT OF VARIOUS ABSORBING AGENTS UPON CORRELATIVE TRANSPIRATION OF WHEAT PLANTS GROWN IN DISTILLED WATER

No.	Treatment	Transpiration	Green weight	Units water transpired per unit green weight (relative)
1	Distilled water, control	100	100	100
2	Distilled water, carbon treated	208	120	173
3	Distilled water, ferric hydrate treated	225	115	196
4	Distilled water, quartz flour treated	245	135	181

These figures show among other things that the proportional transpiration was greatly increased by these treatments. It might be argued logically that the transpiration of the plants in the untreated distilled water is abnormally low, due to the probable presence of poisonous metals in the untreated distilled water, as such substances have the effect of depressing transpiration, while the transpiration of the plants in the treated solutions is normal. The removal of these substances by the absorbing solids leaves the solution in a better physiological condition for plant growth, as evidenced by the increased transpiration and green weight. The same result is also produced to a greater or less extent by redistillation in glass.

Such treatments are generally accompanied by an increased root development, especially in branching, but as a rule this relation is not brought out in the dry weight of the roots, it being often found that a set of long, well-branched roots weigh no more than a set of shorter, more poorly branched roots of the same number of plants, due to the greater thickness of the latter. The weight of the fresh roots would be, however, a more accurate indication of the effect of the treatment, as was shown in table VI. The longer and better branched roots in the culture solutions treated with absorbing solids are to be regarded as indicative of superior conditions for growth, and undoubtedly contribute largely to the increased transpiration.

The general effect of treatment by an absorbing agent in case of soil extracts also is to increase transpiration and root growth of the plants, although there are occasional cases where the increased transpiration is small or negative. Table VIII presents the results of a number of experiments upon this question in which a variety of soil extracts were used. The results of the experiments, made at different times, are presented in terms of the growth of plants grown in control cultures. These control results (not presented in the table) were always taken as 100, and the response to treatment with the absorbing agent expressed by proportional figures.

TABLE VIII

EFFECT ON TRANSPIRATION OF TREATING VARIOUS SOIL EXTRACTS WITH ABSORBING AGENTS BEFORE USING THEM AS CULTURE MEDIA*

No.	Soil extract	Transpiration	Green weight	Units water transpired per unit green weight
1	Elkton silt loam	178	107	167
2	Lyons silt loam	95	121	81
3	Alloway clay	465	147	316
4	Kingston soil	81	83	97
5	Takoma lawn soil	190	104	182
6	Arlington soil	142	110	128
7	Dunkirk sandy loam	96	87	110
8	Memphis silt loam	154	118	129
9	Arlington clay loam	108	110	97
10	Takoma lawn soil	137	109	125
11	Kingston soil	116	109	106
12	Memphis silt loam	117	99	119
13	Dunkirk sandy loam	114	114	100
14	Arlington clay loam	158	102	155
15	DeKalb silt loam	133	103	126
16	Cecil sandy loam	112	97	108
17	Hagerstown loam	229	102	225
18	Dutchess silt loam	110	89	122
19	Cecil sandy loam	193	114	171
20	Lyons silt loam	226	131	181
21	Penn clay	402	111	364
22	Miami black clay loam	142	98	144
23	Miami silt loam	172	123	139
24	Lyons silt loam	626	135	461
25	Park soil	136	97	153
	Average	185.3	108.8	164.2

* The absorbing agent used for treating the first 19 soil extracts was carbon black; for the remainder ferric hydroxid was used.

These results show, almost without exception, that the transpiration and growth were accelerated by previously treating the soil extract with an absorbing agent; also, that the units of water transpired per unit of green growth were greater as a result of the treatment employed. In respect to their effect upon the resulting morphogenesis of the plant, the absorbing agents resemble such substances as pyrogallol.

Discussion and summary

The studies presented in the foregoing pages are devoted mainly to an investigation of the relation of transpiration to the green growth of the plant under the influence of various chemical agents. Higher concentrations of the chemical agents were avoided, since it is well known that a sufficiently concentrated solution of a non-toxic salt will retard growth and produce the effect of a "physiological drought."

The small amounts of the respective chemical agents used had a definite influence upon the correlative transpiration. In the case of lime and sodium phosphate, the transpiration showed material increases, but potassium salts decreased it; while sodium nitrate was somewhat variable, usually operating however to cause a decrease in transpiration. Inorganic acids retarded transpiration, while organic acids were somewhat variable. Pyrogallol and tannic acid resembled the action of absorbing agents in causing large increases in the transpiration per unit of green growth.

These effects appear in all cases to be a specific action of the ions constituting any given agent. For example, K always showed its inhibiting action on transpiration, regardless of whether it was combined with Cl, NO_3, or SO_4; so also was the accelerating action of Ca. In this respect the rôle of these ions is doubtless comparable in specificity with their rôle in nutrition and other physiological processes.

The action of certain of these fertilizer constituents might be, as LAWES suggested, of practical advantage in agricultural operations. Under more or less critical conditions, it is conceivable that the effect of a salt like K_2SO_4, which retards transpiration, might make an appreciable difference in plant growth. An experimental study of this question would be extremely interesting.

There are rather extensive areas where the salts of potassium, but more especially those of sodium, are present in the soil in amounts appreciable to plant life, but insufficient to cause distinct xerophily. Since these areas usually receive scanty rainfall, it is altogether probable that the action of those ions and salts which are here shown to retard the correlative transpiration would play an important part in plant growth.

Concerning the action of pyrogallol and tannic acid, both of which greatly accelerated transpiration, but little remains to be said in this discussion. It may be added, however, that these, or closely related substances, are quite common in plants, and it is conceivable that their presence may influence transpiration independently of other factors. A similar view might be held of the action of oxalic and other organic acids which occur naturally as such in plants.

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